

Face Perception in the Mind's Eye

Ruthger Righart · Nicolas Burra · Patrik Vuilleumier

Received: 6 July 2010 / Accepted: 12 October 2010 / Published online: 4 November 2010
© Springer Science+Business Media, LLC 2010

Abstract Perceptual filling-in occurs when visual stimuli are recognized in impoverished viewing conditions. Whether missing information is filled-in during face perception and which stages might be involved in this process are still unresolved questions. Because an identity can be brought to mind by seeing eyes only, we hypothesized that missing information might be filled-in from a memory trace for the whole face identity. We presented participants with faces in phase 1 and later we presented eyes-only in phase 2. For some of these eyes in phase 2, the whole face had been presented in the previous phase, for others identical eyes had been presented. Event-related potentials (ERPs) revealed an N170 component that was more negative when eyes were preceded by a whole face in the previous phase compared to eyes preceded by identical eyes-only. A more positive-going late positive complex (LPC) was also found, suggesting enhanced retrieval of face memory representations when eyes were preceded by whole faces. Our results show that pre-existing representations of face identity can

influence early stages of visual encoding, 170 ms after stimulus onset. These effects may reflect top-down modulation by memory on visual recognition processes by filling-in the missing facial information.

Keywords Vision · Memory · Top-down modulation · Faces · LPC · N170

Introduction

The realisation that a person has been encountered before may be achieved in a single glance. Even when only partial visual information is seen, such as the eyes, the person behind the eyes can sometimes be recognized when we know her face. This ability might be explained by the fact that the visual system fills-in the critical missing information to evoke the whole face in the mind's eye, even though it is not seen in the actual stimulus.

Several studies have shown that the brain may use top-down processes to interpret information from impoverished views, for instance in order to discriminate faces from objects (Bentin et al. 2002; Cox et al. 2004; Dolan et al. 1997). Dolan et al. (1997) reported that faces and objects that could initially not be identified in fragmented shades of Mooney stimuli, were readily detected after exposure to complete pictures, suggesting that visual information could be completed or interpreted by using previous knowledge. In parallel to improved recognition, PET imaging revealed increased responses in the fusiform gyrus, a region important for face perception, implying that Mooney pictures were now encoded as faces instead of ambiguous images. Using Mooney stimuli as well, George et al. (2005) showed that the N170 amplitude was larger for upright images that were recognized to be faces, as compared with

R. Righart · N. Burra · P. Vuilleumier
Laboratory for Neurology and Imaging of Cognition,
Department of Neuroscience, School of Medicine,
University of Geneva, Geneva, Switzerland

R. Righart · N. Burra · P. Vuilleumier
Swiss Center for Affective Sciences, University of Geneva,
Geneva, Switzerland

P. Vuilleumier
Center for Neuroscience, University of Geneva, Geneva,
Switzerland

R. Righart (✉)
Institute for Stroke and Dementia Research, Klinikum
der Universität München, Max-Lebsche-Platz 30,
81377 Munich, Germany
e-mail: ruthger.righart@med.uni-muenchen.de

upside-down images in which faces were not detected. Likewise, Bentin et al. (2002) showed that two schematic dots, that initially did not evoke a face percept, induced larger N170 amplitudes after subjects had learned that the dots were the eyes of a face (see also Vuilleumier and Sagiv 2001).

Taken together, these studies show that prior knowledge is used for discriminating faces from objects (basic level categorizations), and that specific brain responses increase when participants are inclined to see a face in an otherwise ambiguous image. However, it is not clear whether prior knowledge about a given face identity can also affect early stages of face processing (subordinate level categorizations). Several studies have reported that the N170 is not influenced by face familiarity (Bentin and Deouell 2000; Eimer 2000; Schweinberger et al. 2002; Henson et al. 2003), although others suggested that familiarity (Caharel et al. 2005; Marzi and Viggiano 2007; Jemel et al. 2005) or individuation (Campanella et al. 2000; Jacques and Rossion 2006) can modulate early stages of face perception. Therefore, it remains unresolved whether the N170 activity reflects visual processes sensitive to identity. Familiarity effects are often observed at longer latencies (Bentin and Deouell 2000; Eimer 2000; Schweinberger et al. 2002), rather than for the earlier N170. In particular, shifts in the amplitude of the late positive component (LPC) have been related to recognition memory (Rugg and Curran 2007), with an increased positivity from 300 ms onwards for faces that are repeated after either short (Schweinberger 1995; Schweinberger et al. 2002; Jemel et al. 2005) or long intervals (Curran and Hancock 2007; Yovel and Paller 2004; Joyce and Kutas 2005) between study and test-phase. These effects are consistent with the notion that identity-specific information is encoded at relatively late stages of face processing, following the structural face encoding stages (Bruce and Young 1986).

Furthermore, it is unclear whether early stages of face processing associated with N170 activity are primarily sensitive to essential structural features in faces, as shown by significant responses to eyes presented alone (e.g., Bentin et al. 1996; Schyns et al. 2003; Itier et al. 2007), or whether the N170 activity is related to encoding structural information about a whole individual face shape (Eimer 1998), including identity-specific cues, which can be present even for unknown faces. Several aspects of face-specific effects on the N170 appear to be driven by the eye region (Itier et al. 2007; Bentin et al. 1996, Bentin et al. 2002; Schyns et al. 2003), but are nevertheless influenced by the presence of a surrounding face context (Itier et al. 2007; see also behavioural results by Balas and Sinha 2007), suggesting that the N170 may integrate eye features with configural information from the whole face. This is further suggested by research in which the N170 amplitude

for degraded faces is increased in conditions where participants were exposed to a person's name or a high quality image of a person's face (Jemel et al. 2005).

Classic behavioural data indicate that faces are processed holistically and that a representation of facial identity is retrieved even when the eyes are shown alone (Tanaka and Farah 1993). Participants are better able to reproduce the position of features of a face (e.g., the eyes) when information about the external features (i.e., the outer contours) of the face was available (Balas and Sinha 2007). Thus, behavioural data suggest that participants use information about the whole face from memory to perceive facial features. This is important since pre-existing representations of face identity may play a crucial role in successful recognition when viewing conditions are impoverished.

It is not known whether early processing stages related to the perceptual analysis of faces and/or later stages related to memory are affected by pre-existing representations when only a part of the face is seen. This can be measured using techniques with high-temporal resolution, like event-related potentials (ERPs). To our knowledge, however, no study has thus far investigated whether whole face information can be perceptually filled-in when only the eyes of a known face are seen, and whether this might affect N170 responses, related to perceptual stages, and the LPC, related to memory processes. Here we therefore used ERPs to investigate how filling-in from memory affects these different stages of face processing. Specifically, we examined whether filling-in may occur for eyes when these are seen after exposure to the corresponding whole face in a prior session. We used two phases. In phase 1, participants saw whole faces that could be famous or unknown. In phase 2, eyes were presented, which could correspond to a whole face seen in phase 1 or not. As a control condition, we also presented eyes that were identical (presented alone) in both phases. Based on previous work by Jemel et al. (2005), we hypothesized that the N170 amplitude for eyes in phase 2 would be larger when they were preceded by whole-faces in phase 1, as compared to when they were preceded by identical eyes in phase 1, because the crucial information about face identity could be filled-in from memory traces. As we assumed that the degree of prior experience with faces may influence this filling-in effect, we investigated this for faces that participants had never seen prior to the study (unknown faces) and faces for which participants had already an internal representation (famous faces). In addition to any modulation of perceptual stages as measured by the N170, we also expected that if memory representations are retrieved when eyes are preceded by whole faces, this should be reflected in an enhancement of the LPC activity compared to when eyes are preceded by identical eyes.

Method

Subjects

Participants were 17 students (8 males) from the University of Geneva. All participants ($M = 24.1$ years, 18–39 years) had normal or corrected-to-normal vision and gave informed consent for participation. None reported a history of neurological/psychiatric diseases. One participant was removed from analysis because of excessive EEG artifacts. All participants gave informed consent and the study has been conducted in accordance with the ethical standards laid down in the 1964 Declaration of Helsinki.

Stimuli

Stimuli were frontal greyscale views of unknown and famous faces from the internet. Faces with specific cues that could influence recognition were excluded (facial hair, scars, shades, or paraphernalia like earrings and spectacles).

Another group of subjects ($N = 18$, $M = 23.9$ years, not included in the ERP study) validated a large set of faces using a five-point scale (from 1 = “extremely famous” to 5 = “unknown”). Based on these ratings, a final set of 180 famous faces and 180 unknown faces was selected. The mean rating for the famous faces ($M = 1.96$, $SD = 0.55$) differed significantly from unknown faces ($M = 4.82$, $SD = 0.54$), $F(1,17) = 295.52$, $P < 0.001$. Famous and unknown faces were divided over three different face-sets (balanced for fame and gender), which were counterbalanced for each subject over different conditions.

Eyes were created by taking a rectangular window from the eye-region of the whole face. Stimuli were presented centrally at ~ 80 cm of distance. Height and width of faces were $15.5 \text{ cm} \times 11.5 \text{ cm}$ resp. ($11.2^\circ \times 8.2^\circ$) and the eyes $2.5 \text{ cm} \times 6.9 \text{ cm}$ ($1.8^\circ \times 5^\circ$). Scrambled versions of whole-faces and eyes were made by randomizing the pixels across image space.

Procedure

Subjects were familiarized with a practice session, after which six experimental blocks followed. Each block consisted of two phases (Fig. 1). Phase 1 served as an exposure to whole faces, in order to prime the subsequent presentation of eyes in Phase 2.

As a function of the presentation across the two phases, there were six experimental conditions, each containing 60 trials. The eyes served in different conditions for different subjects to control for potential low-level physical differences between stimulus sets. In two experimental conditions (1 and 2), the eyes seen in phase 2 were preceded by

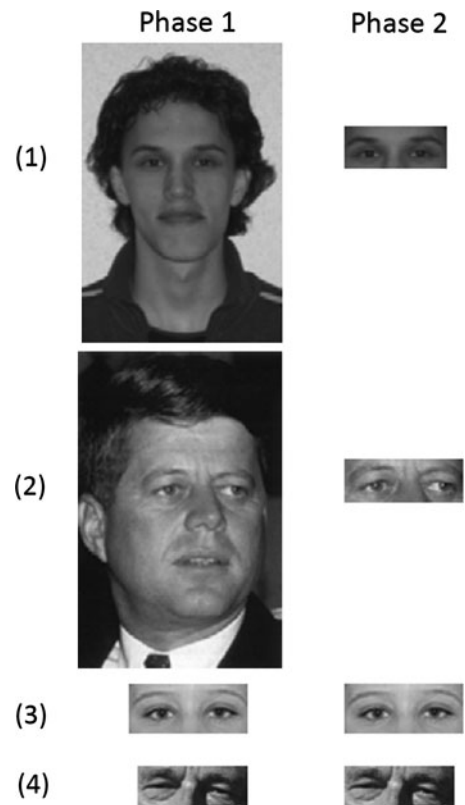


Fig. 1 Experimental paradigm. Stimuli were presented in two phases that were separated by an interval of 2 min. Eyes in phase 2 could be preceded (in phase 1) by a whole face that was either unknown (1) or famous (2), e.g., John F. Kennedy or eyes could be preceded by identical eyes that were taken from an unknown (3) or famous face (4), e.g., Jacques Chirac. Two additional conditions with eyes presented for the first time in phase 2 (from unknown and famous faces) were also used (not shown here) in order to rule out any incidental effects in low-level features or familiarity between unknown and famous eyes

their corresponding whole-face in phase 1. These faces could be either unknown (condition 1) or famous (condition 2). In two other experimental conditions (3 and 4), the eyes in phase 2 were preceded by identical eyes in phase 1, again from either unknown or famous faces. Thus, condition 1 and 2 allowed us to test whether the perception of eyes alone can lead to any filling-in by information retained from prior knowledge of the whole face, and whether such effects differ for already known or previously unknown faces. Critically, these conditions were compared with conditions 3 and 4 to test whether previous perception of the whole face in phase 1 is necessary for filling-in or memory effects on the N170 and the LPC in phase 2, respectively. Two additional experimental conditions (5 and 6) consisted of eyes that were presented in phase 2 only, but intermixed randomly with the other conditions. Since conditions 5 and 6 were presented for the first time, they were not influenced by any general effect of exposure in phase 1, and served to rule out any unwanted low-level

differences between eyes taken from unknown and famous faces (e.g., famous eyes may have intrinsic visual differences due to make-up or evoke differential familiarity responses despite lack of explicit identification), while keeping the task conditions similar across stimuli. It also tests for the possibility whether filling-in effects may occur for famous eyes compared with unknown eyes without any prior presentation of the whole face in phase 1. All six conditions were presented randomly in each block. Each face identity was presented only once to each participant in order to prevent carry-over effects.

Each trial began with a fixation cross (duration jittered 1500–2500 ms), followed by a whole face or eyes (150 ms). In phase 1, subjects had to perform a one-back repetition task in order to ensure that attention was directed to face identity. Subjects were asked to press a button if the same whole face or eyes were repeated from the previous trial. Phase 1 took ~5 min and phase 2 took ~3 min. Phase 2 was directly started up after phase 1 was finished with an approximate time of 2 min between the two sessions. Stimulus presentations and intervals between exposure in phase 1 and presentation of the eyes in phase 2 were randomized for all conditions. In phase 2, presentation-times were identical to phase 1, i.e., 150 ms. Subjects performed an age-decision task for each of the eyes using two response-buttons with their right-hand (younger/older than 45 years), and were encouraged to make their judgment on first impression. Age-decision was used to avoid any attentional effects that could be correlated with the conditions of interest.

Data Acquisition

Electroencephalography (EEG) was recorded during both phase 1 and 2, from 64 electrode locations (BioSemi Active2, active Ag–AgCl electrodes) referenced to an additional active electrode (Common Mode Sense). Horizontal electro-oculographies (EOGs) were recorded from two electrodes placed at the outer canthi of both eyes. Vertical EOGs were recorded from electrodes on the infraorbital and supraorbital regions of the right eye in line with the pupil. EEG was sampled with 1024 Hz and segmented into epochs starting 100 ms before and 800 ms (using 100 ms pre-stimulus baseline) after stimulus-onset, and was bandpass filtered (0.1–30 Hz). An average reference was used for all electrodes.

After EOG correction (Gratton et al. 1983), epochs with amplitudes exceeding 100 μ V at any channel were rejected. ERPs were averaged for each condition. As our primary interest was to study the ERPs to eyes as a function of exposure to whole faces in phase 1, main analyses focused on ERPs to those stimuli in phase 2. We however also report the results for phase 1 to confirm whether results in

the comparison eye-face are replicated from previous studies (Bentin et al. 1996; Itier et al. 2007).

Individual N170 peak amplitudes were determined from occipito-temporal electrode positions (P7/8, PO7/8, and P9/10) using the maximal negative peak centred on a ± 20 ms window relative to the pre-stimulus baseline. LPC mean amplitudes were analyzed for frontal (F5/z/6), fronto-central (FC5/z/6), central (C5/z/6), centro-parietal (CP5/z/6), and parietal sites (P5/z/6), using 100 ms time-windows from 300 to 800 ms.

Data Analysis

Response-times to the age-decision task in phase 2 were averaged for each experimental condition and analyzed with a 2×2 repeated measures ANOVA containing the within-subject factors Celebrity (Famous, Unknown), and Exposure type (Whole, Eyes in phase 1), involving conditions 1–4.

For ERPs in phase 1, the N170 to whole-faces was compared to eyes using a $2 \times 2 \times 2 \times 3$ repeated measures ANOVA with the factors, Stimulus Type (Whole face, Eyes), Celebrity (Famous, Unknown), Hemisphere (Left, Right) and Electrode (P7/8; PO7/8; P9/10). For the N170 in phase 2, the difference between the eyes was analyzed using a $2 \times 2 \times 2 \times 3$ repeated measures ANOVA with the factors Exposure type (Whole face, Eyes), Celebrity (Famous, Unknown), Hemisphere (Left, Right) and Electrode (P7/8; PO7/8; P9/10). Conditions 5 and 6 were analyzed separately so that their novelty (i.e., these stimuli were presented for the first time in phase 2) would not affect the analysis of the other four main conditions (i.e., stimuli repeated after two different types of exposure). Similar factors as for the N170 were used to analyze the LPC, except for electrode position with 5 levels (F5/z/6; FC5/z/6; C5/z/6; CP5/z/6; P5/z/6). To adjust for non-sphericity of variance between conditions, Greenhouse-Geisser epsilon was applied to correct for degrees of freedom (Picton et al. 2000).

Results

Behavioral Results

Performance on the one-back repetition task in phase 1 was almost flawless ($M = 8.0\%$ error). On the age-decision task in phase 2, more eyes were judged older compared with younger than 45, but this was equal across conditions of unknown (Younger $M = 45\%$ vs Older $M = 55\%$) and famous eyes (Younger $M = 46\%$ vs Older $M = 54\%$). No significant differences were found for response-times (overall $M = 747$ ms, $SD = 91$ ms) as a function of

Celebrity, $F(1,15) = 2.61$, $P = 0.13$, and Exposure Type, $F(1,15) = 0.03$, $P = 0.87$.

N170

In phase 1, a main effect of Stimulus type was found on the N170 peak latency, $F(1,15) = 63.56$, $P < 0.001$, showing a significant delay for eyes ($M = 163$ ms, $SD = 12$ ms) compared with whole-faces ($M = 149$ ms, $SD = 13$ ms). For N170 amplitudes, a main effect was also found for Stimulus type, $F(1,15) = 42.84$, $P < 0.001$, with larger N170 amplitudes to eyes ($M = -8.55$ μ V; $SD = 2.66$) than to faces ($M = -5.06$ μ V; $SD = 2.89$). This replicates well-established previous findings (e.g., Bentin et al. 1996; Schyns et al. 2003; Itier et al. 2007). No main effect of Celebrity, $F(1,15) = 1.80$, $P > 0.05$, nor any interaction between Celebrity and Stimulus type was found, $F(1,15) = 0.98$, $P > 0.05$.

In phase 2, the average N170 latencies for eyes peaked at ~ 160 ms. Neither the main effect of Celebrity, $F(1,15) = 0.56$, $P > 0.05$, and Exposure Type, $F(1,15) = 0.57$, $P > 0.05$, nor the interaction between these factors, was significant, $F(2,30) = 0.33$, $P > 0.05$. By contrast, the N170 amplitudes to eyes in phase 2 showed an interaction between Celebrity and Hemisphere, $F(1,15) = 5.91$, $P < 0.05$, which was explained by significant differences between famous ($M = -6.90$ μ V; $SD = 2.85$) and unknown eyes ($M = -6.52$ μ V; $SD = 2.53$) on the right hemisphere, $t(15) = 2.78$, $P < 0.05$. More critically, we observed a significant main effect of Exposure type, $F(1,15) = 5.08$, $P < 0.05$. Planned comparisons indicated that this main effect accorded with our filling-in hypothesis, reflecting an enhancement of N170 by Exposure to whole-face identity, which was numerically (but not significantly) larger for unknown eyes than famous eyes (Figs. 2 and 3). The interaction between Exposure type and Celebrity did not reach significance ($P > 0.05$).

To confirm that the main effect was significant for both unknown and famous eyes, and not driven by one of these conditions alone, we performed planned comparisons (Howell 2002) for unknown and famous eyes separately. For unknown eyes, these planned comparisons showed that N170 amplitudes in phase 2 were significantly larger on the left hemisphere to eyes that were preceded by whole-faces ($M = -6.76$ μ V; $SD = 3.91$) compared to eyes that were preceded by identical eyes ($M = -6.13$ μ V; $SD = 3.90$) in phase 1, for all electrodes of interest on the left hemisphere, $t(15) = 2.21$, $P < 0.05$. A similar difference was observed on the right hemisphere although it was marginally significant, $t(15) = 2.00$, $P = 0.06$. A supplementary 2 (Exposure type) \times 2 (Hemisphere) \times 3 (Electrode) ANOVA confirmed a significant main effect of Exposure type, $F(1,15) = 4.99$, $P < 0.05$, and no significant interaction with hemisphere, $F(1,15) = 0.10$, $P = 0.76$.

For famous eyes, the N170 amplitudes were also significantly larger on the left hemisphere for eyes that were preceded by whole faces in phase 1 ($M = -6.60$ μ V; $SD = 4.05$) compared to those preceded by identical eyes in phase 1 ($M = -6.24$ μ V; $SD = 3.90$), for all electrodes of interest on the left hemisphere, $t(15) = 2.39$, $P < 0.05$ (Fig. 3). These comparisons were not significant for the right hemisphere, $t(15) = 0.51$, $P > 0.05$. Accordingly, a supplementary 2 (Exposure type) \times 2 (Hemisphere) \times 3 (Electrode) ANOVA confirmed an interaction between Exposure type and Hemisphere, $F(1,15) = 6.18$, $P < 0.05$, whereas the main effect of Exposure type was not significant, $F(1,15) = 0.79$, $P = 0.39$. Thus, the filling-in effect was present for both unknown and famous eyes, but surprisingly it appeared larger for unknown eyes than for famous eyes. An additional t -test comparing these filling-in effects (i.e., difference between eyes in phase 2 preceded by a whole face in phase 1 vs. eyes in phase 2 preceded by eyes in phase 1) between unknown ($M = 0.63$ μ V; $SD = 1.14$) and famous eyes ($M = 0.36$ μ V; $SD = 0.60$) had marginal significance, $t(15) = 1.95$, $P = 0.07$. As there was some variation in the age of the participants, we investigated further whether this factor affected the filling-in effect. However, correlation analyses showed no significant correlations between age and the filling-in effect for unknown and famous eyes (all P s > 0.05).

Finally, to test whether incidental differences between unfamiliar and famous eyes might affect the N170 amplitude regardless of exposure history, or whether possible filling-in effects occurred for famous eyes without any prior whole face presentation, we compared eyes that were not presented in phase 1, and for which thus repetition priming effects were not a confounding factor. No significant differences were found between eyes that belonged to unknown and famous faces, neither on the left ($M = -6.25$ μ V; $SD = 3.66$ vs $M = -6.59$ μ V; $SE = 3.61$, respectively, $t(15) = 1.66$, $P > 0.05$), nor on the right hemisphere ($M = -6.70$ μ V; $SD = 2.52$ vs $M = -6.78$ μ V; $SD = 2.71$, $t(15) = 0.28$, $P > 0.05$), suggesting that the exposure effect that was found on the left and (marginally significant) right hemisphere for unknown eyes and on the left hemisphere for famous eyes was unlikely to be confounded by systematic differences in the low-level features and/or familiarity of famous and unknown eyes.

LPC

The analysis of ERPs in phase 2 showed no main effects of Celebrity for any of the time-windows, all P s > 0.05 . More importantly, significant main effects of Exposure type were found between 300–400 ms, $F(1,15) = 5.85$, $P < 0.05$, and between 400 and 500 ms, $F(1,15) = 5.53$, $P < 0.05$, but only marginally between 500 and 600 ms, $F(1,15) = 3.10$,

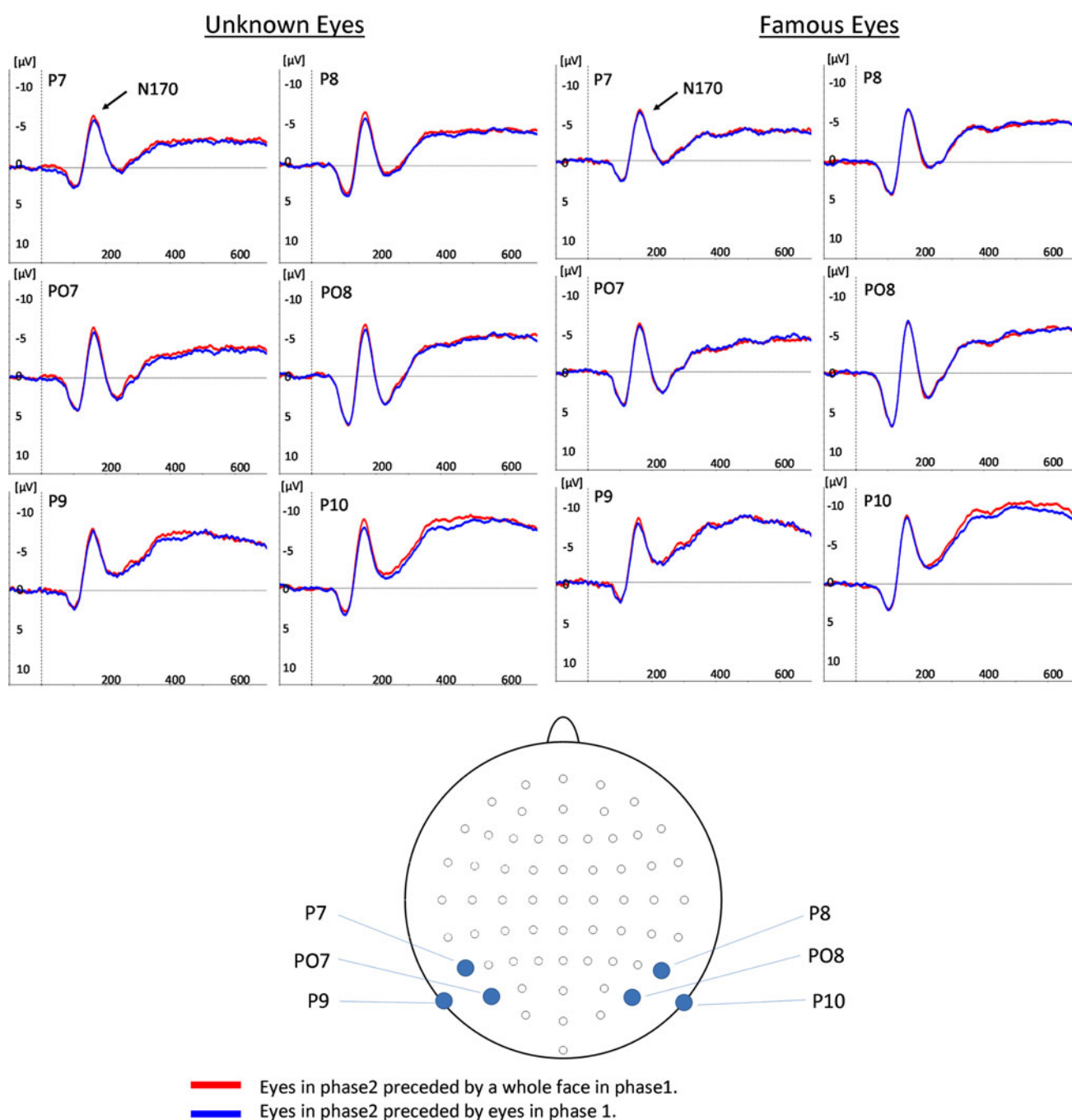


Fig. 2 N170 Grand-average ERP waveforms for unknown and famous eyes in phase 2 at occipito-temporal electrodes on the left and right hemisphere (P7/8, PO7/8, P9/10) are displayed as a function of the exposure type in phase 1 (*red* = whole-face, *blue* = eyes)

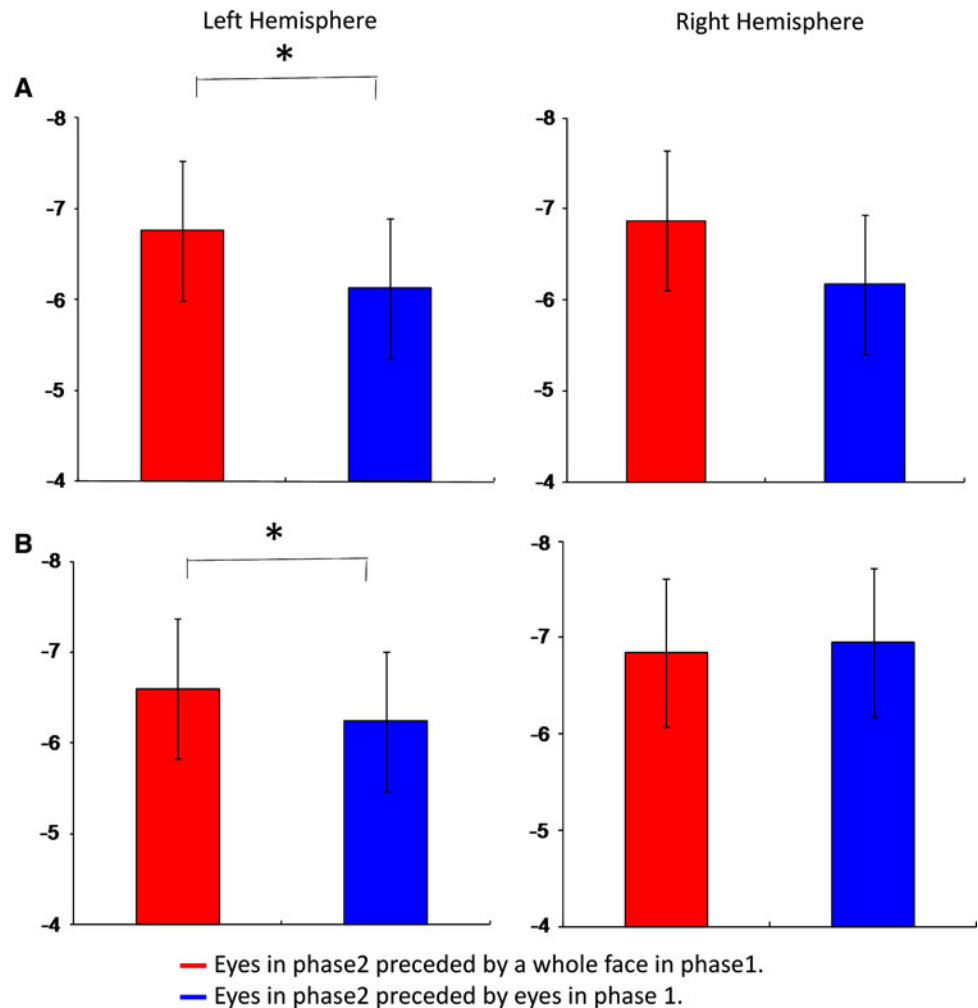
$P = 0.10$. The differences between 600 and 700 ms and between 700 and 800 ms were not significant ($P > 0.05$). These effects reflected more positive-going LPC amplitudes in phase 2 for eyes that were preceded in phase 1 by a whole face compared to those preceded by eyes (Fig. 4). There were no significant interaction effects between Exposure type, Celebrity, Hemisphere and Electrode position for any of the time-windows, all P s > 0.05 . These results suggest that LPC amplitudes to eyes were more positive-going when

subjects were exposed to whole faces, irrespective of whether these were unknown or famous faces.

Discussion

In this study we tested the hypothesis that pre-existing representations of whole face identity could modulate early stages of face processing, even when these representations

Fig. 3 N170 amplitudes for unknown (a) and famous eyes (b) in phase 2. Average N170 amplitudes of peaks were identified on *left* (P7, PO7, P9) and *right* (P8, PO8, P10) occipito-temporal sites for eyes in phase 2, as a function of the Exposure conditions in phase 1. Asterisks indicate significant pairwise comparisons ($P < 0.05$). N170 amplitudes (in phase 2) were larger for eyes that were preceded by a corresponding whole face (in phase 1), over both hemispheres in the unknown condition (but statistically significant for the *left side* only) and over the left hemisphere in the famous condition. Error bars indicate the within-subjects standard error after removal of between-subject variance, according to Loftus and Masson (1994)

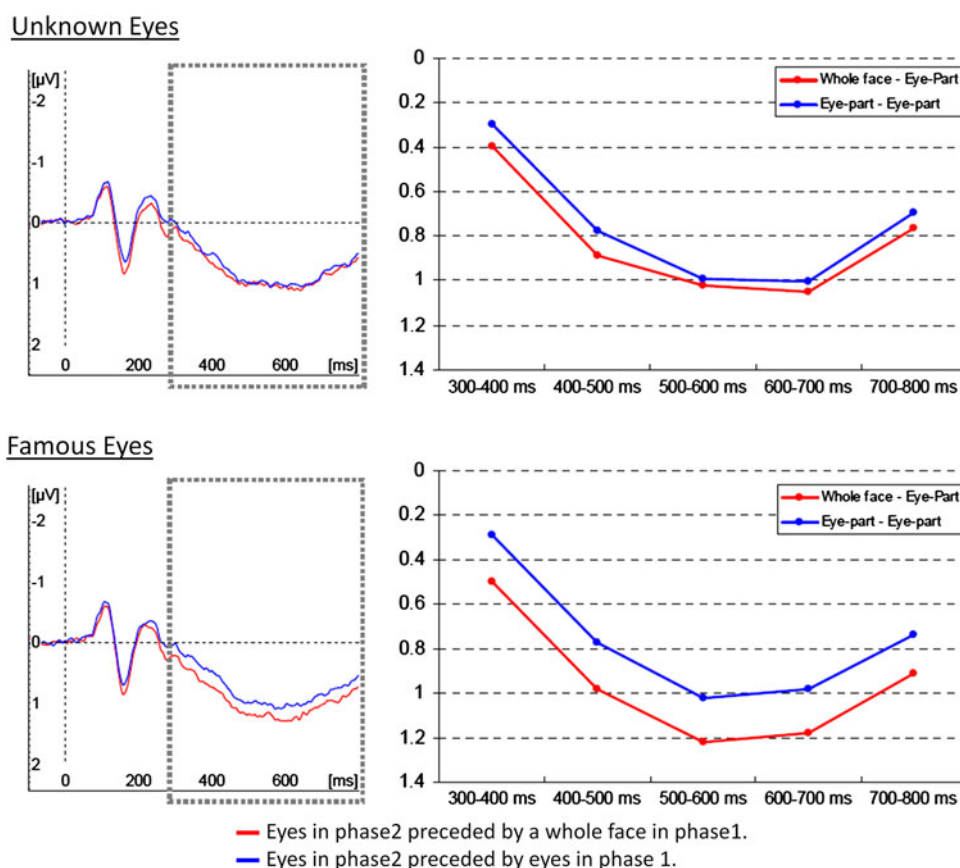


are retrieved from memory by seeing eyes only. Pre-existing representations were formed by exposure to whole faces in phase 1, and compared for already known (famous) and unknown faces, while ERPs from eyes-only were recorded in phase 2. Importantly, the eyes from previously seen faces were compared to eyes that were similarly repeated but never seen with whole-face information, so that any general effect of familiarity or repetition was equal across conditions during re-exposure. In accordance with our prediction, eyes evoked larger N170 amplitudes when they were preceded by whole faces in phase 1. These results indicate that top-down filling-in or completion processes do not only operate for basic-level categorization tasks allowing discrimination of faces from objects in degraded images (Bentin et al. 2002; Cox et al. 2004; Dolan et al. 1997), but they also arise for the subordinate individuation of face identities. Information that is available in memory about external features of known identities is linked with internal features that are perceived, which is consistent with previous behavioral findings (Tanaka and Farah 1993; Balas and Sinha 2007). Furthermore, in

addition to these early influences on perceptual stages (N170), a significant modulation was also found during later processing stages (LPC), which may reflect memory retrieval for previously seen faces.

A major factor that may explain why we found larger N170 amplitudes, rather than a reduction as previously reported for whole face repetition (Henson et al. 2002; Heisz et al. 2006; Itier and Taylor 2004), could be that our stimuli were relatively impoverished in phase 2 (eyes only), which is likely to induce different perceptual mechanisms because impoverished stimuli are more difficult to recognize. This may at the same time explain why the effects were found for both unknown and famous eyes. Previous studies that reported decreased N170 amplitudes after face-repetition (Henson et al. 2002; Heisz et al. 2006; Itier and Taylor 2004) and/or increased LPC amplitudes (Bentin and Deouell 2000; Eimer 2000; Schweinberger 1995; Schweinberger et al. 2002; Henson et al. 2003; Joyce and Kutas 2005) commonly used high quality images of whole faces in which identification was relatively easy. Future studies should investigate whether there is an effect

Fig. 4 Late positive components (LPC). Grand average ERP waveforms (left-side panels) and mean amplitudes (right-side panels) for unknown and famous eyes. For display purposes, ERPs are averaged across 15 electrodes that were used in the LPC analysis (F5/z/6; FC5/z/6; C5/z/6; CP5/z/6; P5/z/6). Mean amplitudes are displayed for consecutive 100 ms time-windows. LPC amplitudes were larger for eyes in phase 2 that were preceded by whole faces in phase 1 (red), as compared with faces preceded by identical eyes (blue)



of degradation on how information is retrieved from memory and how memory traces are used to assist in perception.

Indeed, recent work using face stimuli that were degraded to ambiguous two-tone images has shown that N170 amplitudes were larger when these images were correctly categorized as being faces (George et al. 2005). Another study using a priming paradigm showed that perception of degraded stimuli (i.e., two-tone images of faces) was modulated by exposure to crucial information that revealed the face identity (i.e., printed name or high quality picture of the face) and produced increased N170 amplitudes (Jemel et al. 2005). These results suggest that when stimuli are impoverished, perceptual encoding processes reflected by the N170 may be enhanced by prior knowledge. The current data show that filling-in or completion may not necessarily be based on the perception of face contours but also arise for eyes-only (see also Jemel et al. 2005).

Our findings show that the N170 does not only relate to categorical face encoding (Bentin and Deouell 2000; Bentin et al. 2002; Eimer 2000) or to the mere extraction of basic facial features such as the eyes (Schyns et al. 2003; Itier et al. 2007). Rather, it reflects a more complex perceptual process beyond categorization, that is sensitive to

face identity (Jemel et al. 2005; see also Campanella et al. 2000; Jacques and Rossion 2006) and that this level of processing is significantly influenced by information stored in memory. Such memory influences were presumably mediated by perceptual representations of previously seen faces, rather than long-term semantic knowledge, because we found that the N170 was larger when eyes could be “enriched” by memory for both famous and unknown identities. This memory effect on the N170 is therefore consistent with recent work that has shown an increased N170 amplitude for faces that were held in working memory (Sreenivasan et al. 2007) or faces that were visualized (Ganis and Schendan 2008), but goes beyond these results by showing that similar effects can be obtained without explicit task demands on memory or identification, and can arise with parts of previously seen faces rather than repetition of the whole stimulus.

In addition, we found that the LPC (300–500 ms) was also modulated by the exposed whole-face, providing further support to the notion that a stronger memory representation could be formed and/or retrieved in this condition relative to when a representation about whole-face identity could not be retrieved (i.e., eyes in phase 2 that were preceded by identical eyes in phase 1). A larger positive-going LPC has been interpreted as a neural correlate of

recognition memory and person knowledge (Rugg and Curran 2007). Here, however, no differences were found for the LPC between famous and unknown eyes. A few studies have shown that the LPC is more positive to familiar than unfamiliar whole faces (Curran and Hancock 2007; Joyce and Kutas 2005; Yovel and Paller 2004), even when individuals are not aware that they had seen faces before (Schweinberger 1995; Seeck et al. 1997). Nevertheless, our results are consistent with those of Jemel et al. (2005) who observed no significant difference from 400 to 600 ms between unfamiliar and famous faces that were previously primed with the same-person. This lack of a difference between famous and unknown faces may indicate that our effects are not based on long-term semantic memory representations for faces (in which case the LPC should probably be increased for famous faces), but instead that these effects are more likely to rely on short-term memory traces that were formed for both famous and unfamiliar faces.

Another factor in addition to short-term memory that may have affected the N170 and LPC is mental imagery. Mental imagery might be an effective means by which missing information in degraded stimuli is filled-into support recognition (Kosslyn 1994). Note that we chose task conditions that were orthogonal to face identification to avoid that attentional effects could explain our results. We however contend that the task of age-decision evokes these memories or mental images of faces implicitly. Previous studies accord with the notion that mental imagery recruits early visual as well as high-order brain regions (Farah et al. 1989; Rhodes and Donaldson 2008), which has been as well shown for faces (Ishai et al. 2000; Ganis and Schendan 2008). The current hemispheric asymmetry on the N170 is consistent with previous studies on mental imagery, which found increased neural activity in left visual areas when subjects generated mental images for words (Farah et al. 1989) and faces (Ishai et al. 2000).

Because many natural viewing conditions may be challenging for our visual system, top-down modulation from internal representations is likely to play a vital role for successful recognition of objects or faces in many real life conditions (Bar 2003; Cox et al. 2004). Human observers often show striking identification accuracy in situations where crucial information is missing (Sinha 2002). Our study provides new insight into the neural underpinnings of such efficiency by showing that the brain can use stored memory representations to guide early stages of face recognition in impoverished viewing conditions.

Acknowledgments This research was supported by the Swiss National Centre of Competence in Research (NCCR) for Affective Sciences, and grants of the Swiss National Science Foundation to PV. We thank Andres Posada for assistance with the EEG set-up and two anonymous reviewers for their helpful comments on the manuscript.

References

- Balas BJ, Sinha P (2007) Portraits and perception: configural information in creating and recognizing face images. *Spat Vis* 21:119–135
- Bar M (2003) A cortical mechanism for triggering top-down facilitation in visual object recognition. *J Cogn Neurosci* 15:600–609
- Bentin S, Deouell LY (2000) Structural encoding and identification in face processing: ERP evidence for separate mechanisms. *Cogn Neuropsychol* 17:35–54
- Bentin S, Allison T, Puce A, Perez E, McCarthy G (1996) Electrophysiological studies of face perception in humans. *J Cogn Neurosci* 8:551–565
- Bentin S, Sagiv N, Mecklinger A, Friederici A, Von Cramon Y (2002) Priming visual face-processing mechanisms: electrophysiological evidence. *Psychol Sci* 13:190–193
- Bruce V, Young A (1986) Understanding face recognition. *Br J Psychol* 77:305–327
- Caharel S, Courtay N, Bernard C, Lalonde R, Rebai M (2005) Familiarity and emotional expressions influence an early stage of face processing: an electrophysiological study. *Brain Cogn* 59:96–100
- Campanella S, Hanoteau C, Depy D, Rossion B, Bruyer R, Crommelinck M, Guerit JM (2000) Right N170 modulation in a face discrimination task: an account for categorical perception of familiar faces. *Psychophysiology* 37:796–806
- Cox D, Meyers E, Sinha P (2004) Contextually evoked object-specific responses in human visual cortex. *Science* 304:115–117
- Curran T, Hancock J (2007) The FN400 indexes familiarity-based recognition of faces. *Neuroimage* 36:464–471
- Dolan RJ, Fink GR, Rolls E, Booth M, Holmes A, Frackowiak RS, Friston KJ (1997) How the brain learns to see objects and faces in an impoverished context. *Nature* 389:596–599
- Eimer M (1998) Does the face-specific N170 component reflect the activity of a specialized eye processor? *Neuroreport* 9:2945–2948
- Eimer M (2000) Event-related brain potentials distinguish processing stages involved in face perception and recognition. *Clin Neurophysiol* 111:694–705
- Farah MJ, Weisberg LL, Monheit M, Peronnet F (1989) Brain activity underlying mental imagery: event-related potentials during mental image generation. *J Cogn Neurosci* 1:302–316
- Ganis G, Schendan HE (2008) Visual mental imagery and perception produce opposite adaptation effects on early brain potentials. *Neuroimage* 42:1714–1727
- George N, Jemel B, Fiori N, Chaby L, Renault B (2005) Electrophysiological correlates of facial decision: insights from upright and upside-down Mooney-face perception. *Cogn Br Res* 24:663–673
- Gratton G, Coles MGH, Donchin E (1983) A new method for off-line removal of ocular artifact. *Electroencephalography Clin Neurophysiol* 55:468–484
- Heisz JJ, Watter S, Shedden JM (2006) Automatic face identity encoding at the N170. *Vis Res* 46:4604–4614
- Henson RN, Shallice T, Gorno-Tempini ML, Dolan RJ (2002) Face repetition effects in implicit and explicit memory tests as measured by fMRI. *Cereb Cortex* 12:178–186
- Henson RN, Goshen-Gottstein Y, Ganel T, Otten LJ, Quayle A, Rugg MD (2003) Electrophysiological and haemodynamic correlates of face perception, recognition and priming. *Cereb Cortex* 13: 793–805
- Howell DC (2002) Statistical methods for psychology, 5th edn. Duxbury, Pacific Grove, CA
- Ishai A, Ungerleider LG, Haxby J (2000) Distributed neural systems for the generation of visual images. *Neuron* 28:979–990
- Itier RJ, Taylor MJ (2004) Effects of repetition learning on upright, inverted and contrast-reversed face processing using ERPs. *Neuroimage* 21:1518–1532

- Itier RJ, Alain C, Sedore K, McIntosh AR (2007) Early face processing specificity: it's in the eyes!. *J Cogn Neurosci* 19:1815–1826
- Jacques C, Rossion B (2006) The speed of individual face categorization. *Psychol Sci* 17:485–492
- Jemel B, Pisani M, Rousselle L, Crommelinck M, Bruyer R (2005) Exploring the functional architecture of person recognition system with event-related potentials in a within- and cross domain self-priming of faces. *Neuropsychologia* 43:2024–2040
- Joyce C, Kutas M (2005) Event-related potential correlates of long-term memory for briefly presented faces. *J Cogn Neurosci* 17:757–767
- Kosslyn S (1994) *Image and brain: the resolution of the imagery debate*. MIT Press, Cambridge, MA
- Loftus GR, Masson MEJ (1994) Using confidence intervals in within-subject designs. *Psychon Bull Rev* 1:476–490
- Marzi T, Viggiano MP (2007) Interplay between familiarity and orientation in face processing. An ERP study. *Int J Psychophysiol* 65:182–192
- Picton TW, Bentin S, Berg P, Donchin E, Hillyard SA, Johnson R Jr (2000) Guidelines for using event-related potentials to study cognition: recording standards and publication criteria. *Psychophysiology* 37:127–152
- Rhodes S, Donaldson DI (2008) Electrophysiological evidence for the effect of interactive imagery on episodic memory: encouraging familiarity for non-unitized stimuli during associative recognition. *NeuroImage* 39:873–884
- Rugg MD, Curran T (2007) Event-related potentials and recognition memory. *Trends Cogn Sci* 11:251–257
- Schweinberger SR (1995) Repetition priming and associative priming on face recognition: evidence from event-related potentials. *J Exp Psychol: Learning Memory Cogn* 21:722–736
- Schweinberger SR, Pickering EC, Jentzsch I, Burton AM, Kaufman JM (2002) Event-related potential evidence for a response of inferior temporal cortex to familiar face repetitions. *Cogn Brain Res* 14:398–409
- Schyns PG, Jentzsch I, Johnson M, Schweinberger SR, Gosselin F (2003) A principled method for determining the functionality of brain responses. *Neuroreport* 14:1665–1669
- Seeck M, Mainwaring N, Cosgrove MD, Blume H, Dubuisson D, Mesulam M-M, Schomer DL (1997) Neurophysiologic correlates of implicit face memory in intracranial visual evoked potentials. *Neurology* 49:1312–1316
- Sinha P (2002) Recognizing complex patterns. *Nature Neurosci* 5:1093–1097
- Sreenivasan KK, Katz J, Jha A (2007) Temporal characteristics of top-down modulations during working memory maintenance: an event-related potential study of the N170 component. *J Cogn Neurosci* 19:1836–1844
- Tanaka JW, Farah MJ (1993) Parts and wholes in face recognition. *Q J Exp Psychol Section A* 46:225–245
- Vuilleumier P, Sagiv N (2001) Two eyes make a pair: facial organization and perceptual learning reduce visual extinction. *Neuropsychologia* 39:1144–1149
- Yovel G, Paller K (2004) The neural basis of the butcher-on-the-bus phenomenon: when a face seems familiar but is not remembered. *Neuroimage* 21:789–800